Executive Summary of Empirical Findings

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Introduction

A research initiative was conducted from 1994 to 1999 in Rocky Mountain National Park (RMNP), Colorado, to evaluate the numbers, trends, and ecological effects of elk (*Cervus elaphus*) in the park and the adjacent Estes Valley. Concerns were expressed that perhaps too many elk inhabited the area, that animals were over-concentrated in certain locales, and that certain vegetative changes were taking place. In particular, concerns were expressed over the visual appearance of short, hedged willows in the open wet meadows on the park primary elk winter range.

Elk were extirpated, or nearly so, from RMNP by human exploitation in the late 1800s, but were reintroduced in 1913 and 1914. Elk steadily increased until they reached an estimated 1,000 animals within the park boundaries in 1944 (Packard 1947). Due to concerns over increasing elk numbers and potential effects on the park winter range, elk in the park were artificially reduced from 1943 to 1968. During this period, 1,664 elk were removed from the park with the goal of reducing the park herd to about 400–500 on the winter range on the eastern side of the park. In 1968, elk were no longer controlled within the park's boundaries, in concert with an NPS change in management policy to one of natural regulation that occurred in Yellowstone National Park at the same time. From 1968 to the present time, increasing reliance to limit the herd was placed on harvests outside of the park. Interagency goals of the National Park Service (NPS), Colorado Division of Wildlife (CDOW), and U.S. Forest Service (USFS) included use of both regular and late season hunts outside of the park boundaries to limit the elk population. A goal was set to harvest 500–600 elk each year that was based on a population reconstruction harvest model (called POP-II). This goal was set with the intent to limit growth of the elk population. This goal of harvesting 500–600 elk was nearly achieved prior to 1987, when an average of 442 ± 78 elk were harvested each year, but after 1987, increasing restriction to private lands outside the park functioned to reduce the ability to harvest the desired number of elk. Elk harvests declined to 302 ± 36 following 1987 through 1996. The more recent use of the town area, and habituation of elk to humans there, have also made elk increasingly inaccessible to sport hunters. Although the harvests may have slowed elk population growth, the desired limitation was never achieved and elk steadily increased both in the park since 1968 and in the town of Estes Park after elk pioneered the town area in the late 1970s (Chapter 1). By 1993, concerns over high elk numbers resulted in criticism of the park elk policy (Hess 1993) and led the agencies to re-evaluate their interagency elk management efforts. In 1993, the park superintendent, James Thompson, requested F. J. Singer (of the U.S. Geological Survey, Biological Resources Division, then the National Biological Service) to conduct a problem analysis of the elk situation and then to write a proposal to research the elk situation.

The goals of the study included providing park managers with information on the effects that elk were having on plant species and the ecosystem. At the onset of the study, it was recognized that a number of human influences had occurred in the system that might confound the interpretation of the effects of the elk abundance alone. For example, any climate change or unnatural succession due to fire suppression by park management might have influenced plant communities. A number of meadows in the winter range had been drained for a golf course in the park (now gone since the 1960s) and for agriculture at a few homesteads within the park. Beaver had apparently declined both on and off the winter range, for unknown reasons. The presence of the rapidly growing town of Estes Park, located within the winter range, might have altered or abbreviated elk migrations. The major predators of the system, wolves and grizzly bears, had long since been extirpated and considerable debate and speculation surrounded what their effects might have been on ungulate populations in a pristine system.

National Park Service (NPS) policy states that natural processes should be relied upon to the largest extent possible to manage wildlife populations within national parks, but that high populations of animals may be managed, if those over-concentrations are due to human activities (NPS 2001). Human activities may have altered some national park ecosystems from their preexisting, unaltered, naturally functioning state. Native predators have been eliminated from many national parks, migrations of ungulates have been altered by developments and activities outside of parks, keystone predators have been eliminated, and climate change potentially due to human activities may have altered ecosystems (Wagner et al. 1995; Wright 1996; Singer et al. 1998a). NPS guidelines do not provide specific criteria by which to evaluate potential ungulate overabundance.

The assessment of what constitutes an over-concentration or too much grazing by ungulates in a national park is a very complex question. Overgrazing is typically defined as any excess of herbivory that leads to degradation of plant and soil resources. However, even in this simplest of definitions, the word "excess" is a value-laden term that may be defined differently depending upon one's objectives in managing an ecosystem. A range manager, wildlife manager, ecologist, or park manager might have very different management objectives for ungulates and each might define an "excess" differently. Ungulate grazing nearly always results in some effects on the plant and the ecosystem, but when do those effects become too much?

The purpose of this research was to document the influences that elk had on the RMNP ecosystem for managers, but not to make any judgments as to what effects were acceptable or unacceptable. The criteria for five commonly-used ecological approaches to evaluate the abundance of ungulates (the population based-predator limitation, the allowable use, the overgrazing, the grazing optimization/sustainability, and the biodiversity approaches) are presented in Chapter 12 and their potential for ease of application to park management situations is discussed. Each one of these approaches has some potential for application to the RMNP elk assessment.

In 1993 and through 1999, the Biological Resources Division of the U.S. Geological Survey, Midcontinent Ecological Science Center (then the National Biological Service), in conjunction with the National Park Service Natural Resources Preservation Program and RMNP, conducted a series of research studies into the question of the possible overabundance of elk in the park. The broad objectives addressed in the initiative included the following: (1) to determine the current status and trends, population demography (survival and recruitment), and distributions of elk on winter range in both the park and in town; (2) to determine current vegetation conditions and trends on the winter range; (3) to evaluate the relative effects of elk herbivory, water additions, artificial clipping, and fire on vegetative conditions; (4) in a general sense, to assess the role of water availability and precipitation patterns; (5) to evaluate the long-term effects of grazing on soil fertility and the sustainability of the system; and (6) to conduct modeling experiments to predict effects resulting from different management scenarios.

Specific projects addressed in the combined USGS-NPS initiative included the following:

Elk Population Studies

1. Aerial and ground estimations of elk densities were conducted in the park and town, assisted with information from marked animals from the capture and radiocollaring of 73 elk during 1995 (Chapter 1). An aerial sightability model was developed in the park and a mark-resight model in the town to estimate elk numbers.
2. Estimates of elk survivorship and recruitment were developed from these population estimates and the radiocollared animals. Population models were developed for the park and town elk subpopulations. These models were then used to develop population-based estimates of food-limited ecological carrying capacity (ECC or K)[a] for elk in both sectors. (Chapter 1).
3. In order to calculate an independent forage-based estimate of K for elk in the town sector, forage biomass was sampled in 1997, 1998, and 2000 in town (Chapter 12). A prior estimate of the park's capability of vegetation and forage nutrition to support elk was provided in earlier research by the Colorado Division of Wildlife (Hobbs et al. 1982).

[a]Food-limited carrying capacity (K) is defined as the ungulate-vegetation ceiling for an area. This is the number of ungulates that the area can support, where the ungulates are regulated by density-dependent processes set by per capita restrictions in food availability. Density-dependent processes that can act to regulate the population might include decreased survival, decreased recruitment, or increased dispersal at higher densities. Predators limit ungulates below K in many ecosystems. Evidence has been reported for multi-predator (usually wolves and bears together) limitation of ungulates (Gasaway et al. 1992; Messier 1994; Orians et al. 1997; Peterson 1999). Limitation is more likely when there is more than one species of major predator (Orians et al. 1997).

Landscape Level Measures

1. Long-term trends in vegetation were determined on the open winter range using the long-term plots monitored from 1968 to 1992 (Chapter 3).
2. A series of 25 additional willow plots were randomly located across the landscape of the winter range and monitored during the study for condition and trend (Chapter 12).
3. The historical trends in stream channel patterns and willow cover since the 1940s were assessed using GIS, photo interpretations, and ground truthing (Chapter 2). The historical trends in the abundance of beaver and their ponds were assessed from repeated ground surveys of active dams, food caches, and lodges since 1939 (Chapter 4).

Treatments and Experiments[b]

1. Twelve new exclosures were erected in willow communities (stratified into short and tall willows) in 1994. Check dams were placed in streamside channels at some of the sites, and artificial clipping was used to simulate higher levels of herbivory inside the exclosures. A control, or undisturbed, plot was maintained inside of each exclosure. An additional four new exclosures were erected in upland shrub communities in 1995. Prescribed burns were conducted inside and outside portions of these exclosures in 1995–1996 (Chapter 4).
2. A large number of variables were measured for each treatment, including any changes in depth to the water table, plant species composition, plant production, responses in willow morphology and community structure, and responses in nutrient concentrations of plants (Chapters 4 and 5); plant ecophysiology responses (Chapters 6 and 8); secondary metabolites or plant defense compounds (Chapter 9); and patterns in isotopic signatures of carbon and oxygen (Chapter 7).
3. Measurements of plant, soil, and process responses were taken at three long-term (35-year) exclosures and adjacent grazed sites on the elk winter range in the park (Chapters 10 and 11).
4. Climate and stream flows were monitored during the study. An analysis of long-term trends in climate patterns for the area was reported in an earlier publication (Singer et al. 1998b).

Ecosystem Sustainability to Grazing by Ungulates

1. The effect of elk upon soil fertility and long-term sustainability of the ecosystem was also assessed. The dynamics of nitrogen (N), a nutrient often in limited supply that may strongly influence plant growth, and carbon (C), in response to elk activity was documented. We studied the removal of N and C by elk grazing, the annual inputs of N and C by the plants following the grazing removals, the annual inputs of N and C from elk urine and feces, the transport of N from the summer range, and the loss of N and C from certain vegetation types on the winter range due to elk herbivory (Chapter 11).
2. The CENTURY soil model was used in the sustainability analysis to predict the responses of N and C to elk herbivory (Chapter 11).

Computer Simulation Modeling

1. The SAVANNA ecosystem model was applied to predict the effects that human alterations have had on the ecosystem and to project the effects of different management scenarios (Coughenour 2001).

The majority of the research was conducted by scientists from the Natural Resource Ecology Laboratory at Colorado State University. Researchers also represented the Statistics and Fisheries and Wildlife Departments of Colorado State University, the Botany and Range Science Department of Brigham Young University, and the Midcontinent Ecological Science Center of the U.S. Geological Survey. The chapters in this final report consist of individual manuscripts that address all of the empirical findings from the 1993–1999 elk initiative. The full results from the ecosystem simulation modeling are presented independently, in a technical report to the USGS-BRD and the NPS

[b]The purpose of the experiments was to control for all other potentially confounding influences and factors such as herbivory by small mammals and insects, succession, and others, by applying the main treatment effect (fencing, damming, clipping, burning) to one of two similar macro plots. In this study, both the study site and the macro plot that received the treatment were selected by random procedures.

(Coughenour 2001); however, the executive summary from that report is included at the end of this final report.

This executive summary features key findings from the empirical studies. Space in this summary is insufficient to review each and every one of the findings here. Please refer to the specific chapters in the report for greater details.

Key Findings

Elk Populations and Distributions

The studies revealed three largely distinct subpopulations of elk on the primary winter range: (a) the Moraine Park-Beaver Meadows; (b) the Horseshoe Park; and (c) the town of Estes Park subpopulations. A few animals wintered in the small Cow Creek area, also part of the park winter range, and another 125 or so animals spent the winters on windswept alpine meadows of Trail Ridge (Chapter 1). Elk densities were about three times higher in the Moraine Park-Beaver Meadows area than in the Horseshoe Park area, both which are within park boundaries. Average elk densities across the winter range varied dramatically. Average elk densities in the park during all aerial surveys, 1994–1999, were very high, >65 elk/km^2 (range = 66–110 elk/km^2) on 2.9 km^2 (3%) of the winter range; high, 30–65 elk/km^2 on 4.0 km^2 (4%) of the winter range; but medium, 10–29 elk/km^2 or low, <1–9 elk/km^2 on the remaining 92.5km^2 (93%) of the winter range (Chapter 12).

The park elk population grew rapidly following release from controls in 1968, but the elk population growth began to slow about 1980, and stabilized ($\lambda \cong 1.0$) at about 1,000 animals in 1990 due to lowered calf and yearling survival rates. The population based *K* for the park subpopulations was 1,069 $\pm$ 55 ($\bar{x} \pm$ SE) elk (Chapter 1). This estimate compares favorably with the forage-nutritional based average estimates of 991 $\pm$ 102 for a slightly dry year and 1,481 $\pm$ 261 elk for a wet year reported by Hobbs et al. (1982) for the park area.

The 2001 modeled population estimate for the Estes Park town subpopulation was 1,975 $\pm$ 150 elk (Chapter 1). This sector of the elk population was still growing at about 5.2% per year at the end of the study. The population-based estimate of *K* for the town, i.e., its potential largest size at the vegetation ceiling, is 2,869 $\pm$ 415 elk (Chapter 1). This compares favorably with independent forage based maximum elk potential estimates of 2,330 ± 78 to 2,563 $\pm$ 85 elk for a dry year and 3,082 ± 103 to 3,391 $\pm$ 113 elk for a normal year (Chapter 12). These potentials for elk populations in town will continue to decline as human developments remove useable elk habitat. I concluded *K* for elk were well approximated for both the park and the town sectors, due to the application of the various methods, but the reader should be reminded that these are estimates only and also that *K* will vary due to climatic conditions. Ecological carrying capacity for the potential largest size for the entire population was about 3,938 $\pm$ 419 elk (Chapter 12). Adult annual survival rates for cows were about 0.913 in both the park and the town sectors. Adult bull survival was 0.79 in the park, but only 0.42 in town due to sport harvests (Chapter 1).

Current Vegetation Conditions and Trends

The USGS-CSU study team generally found no effect on plant species diversity in upland shrub and willow communities in the 4-year exclosures (no differences were found in the six treatment types; Chapter 12). This finding of no or few diversity differences was also supported by two independent samplings at the older, 35-year exclosures by Tom Stohlgren (USGS-MESC) and his coworkers in 1997 (Stohlgren et al. 1999) and at these older exclosures by our study team in 1998 (Chapter 12). The wet meadow, willow, upland shrub, and Ponderosa pine/shrub types were well represented by these samplings. However, in contrast to our samplings, Dave Stevens, (now retired NPS) found that, following more than 25 years of grazing, three less palatable plants (*Carex* spp., *Selaginella densa*, *Phleum pratense*) increased on heavily grazed and dry open upland grass/shrub and meadow sites (Chapter 3, also see Stevens [1992]). This latter study, however, did not include sampling in control, i.e., ungrazed sites, and thus, effects of confounding variables such as climate and succession cannot be ruled out. The upward trends of several less palatable plant species through time on these grazed sites may warrant further consideration.

Based on published information from similar ecosystems, the elk consumption rates (~60%) on herbaceous vegetation in the upland grass/shrub type appeared relatively high from the viewpoint of conventional guidelines for allowable use (Chapter 12). A general guideline for sustainable range management is for maximum consumption of herbaceous vegetation to be about 50%, while substantially higher levels result in species and ecosystem alterations (see Biondini et al. [1998] for results of a test of the 50% rule). There was little predictability from the literature of the effects from shrub use values in any of the types we studied, since so many of the studies used artificial clipping to simulate herbivory. We found the effects of natural elk herbivory were much greater than clipping, apparently due to the stripping of bark and the rough breakage of willow stems by elk (Chapters 4 and 6). Willow structure and growth declined noticeably at use levels of about 37% by the wild elk and greater (Chapter 12). The structural changes attributed to elk herbivory at these higher use levels in the willow type were quite large (Chapters 4, 5, and 11). Overall, consumption of willows on the winter range averaged 33% by elk (Chapter 12).

A number of additional plant community alterations were also attributed to elk herbivory. At the 4-year exclosures in the willow type, there was 4.6% more bare ground on the grazed sites (7.7% grazed vs. 3.1% ungrazed), herbaceous production declined 22%, and there were less bluebell (*Mertensia ciliata*) and more *Solidago* spp. on the grazed sites. In grazed upland grass/shrub sites, cover of *Artemisia ludoviciana* was reduced 62% and cover of *Eriogonum umbellatum* was 50% less on grazed sites (Chapter 12). At the 35-year exclosures, the size and production of big sagebrush (*Artemisia tridentata*), an upland shrub that covers about 5–8% of the winter range, was reduced by two-thirds. However, size and production of the much more ubiquitous bitterbrush (*Purshia tridentata*) increased on grazed sites. The trend toward slightly more bare ground continued at the 35-year exclosures where there was 6.4% more bare ground on grazed sites compared to ungrazed sites (this difference, however, was not statistically significant; Chapter 12).

Willow production was reduced 66% by year 4 of the study (Chapter 4). There were no effects on willow production in years 1–3 (Chapters 4 and 5), which were years with heavy snowpacks and high stream runoff. In year 4 (1998), following a more normal spring stream runoff, willow community production was significantly less in grazed treatments compared to the ungrazed controls (Chapter 4). I attribute the differences in reported findings either to the difference in years of measurements (Raul Peinetti did not sample in 1998) or to the individual-willow-based sample of Peinetti et al. (Chapter 5) vs. the plot-based sample of Zeigenfuss et al. (Chapter 4). Additionally, willow catkins were reduced 70%, there were fewer shoots/grazed stem, and there were fewer leaves/grazed stem (228 vs. 411) in grazed willows (Chapters 4 and 5). Another effect of elk herbivory was that grazed willows obtained less of their water from groundwater than did ungrazed willows based on isotope analysis (Chapter 8). These authors concluded from the isotopic signatures that willows growing on sites further removed from streamsides likely possessed reduced rooting depths and thus were less able to compensate for the effects of the intense herbivory than streamside and ungrazed willows.

Grazed willows also possessed heavier and longer shoots, more shoots and more leaves per unit of biomass, and there was more current biomass (n) per unit of previous year's (n-1) biomass. There were few physiological differences, but large morphological and canopy architecture structural differences between grazed and ungrazed willows. Vigorously grazed willows tended to "catch-up" in size during the growing season to ungrazed willows (Chapter 5), but overall, grazed willows were significantly shorter than ungrazed willows by the end of the study (Chapters 4 and 5). Grazing optimization, a curvilinear relation with peak values at moderate herbivory, was verified for eight different willow growth parameters on the RMNP winter range. The evidence for this grazing optimization included the following. At moderate levels of willow consumption (about $21 \pm 0.4\%$ annual use), willow growth parameters exceeded those for ungrazed willows, but at high levels of use ($>37 \pm 3\%$ use) willow growth parameters declined. Moderately browsed willows (browsed at about 21% of current annual growth) produced substantially more current annual growth, stems were more dense, plants were taller on the average, and canopy volume was greater than for their unbrowsed counterparts (Chapter 12).

The high consumption rate of 37% of the annual growth of willows corresponded to a high density of $\sim 32 \pm 1$ elk/km^2. At these and higher elk densities and herbivory levels, elk were having a negative influence on willows (Chapter 12). These negative effects were occurring on large portions of Moraine Park where elk densities were very high, and on some portions of Horseshoe Park (Chapter 12).

The Relative Role of Elk Herbivory, Water, and Prescribed Fire Evaluated from Experiments

The experiments with exclosures, indicated elk herbivory suppressed willow heights, leader lengths, and annual production in the short willow type, as well as reduced herbaceous biomass production by about 22%. The water impoundment treatments increased graminoid production over controls on the drier sites, but the impoundment treatments did not significantly influence shrub production. The researchers suspected that the impoundment treatment was of too short duration in the growing season (only about six weeks of dam effects) and the natural water tables were high (no water table fell below 1 m even in late summer on any site), even on sites formerly occupied by beaver and with no active impoundments, to influence the shrubs (Chapter 4).

Prescribed burning in the upland bitterbrush communities decreased the amounts of shrub cover and production, at least in the short-term of the study, but there was no effect on herbaceous standing biomass, except that biomass of *Stipa comata* declined. However, grazing in the upland grass/bitterbrush type reduced herbaceous biomass, increased N content of grasses, and increased digestibility of grasses and forbs (Chapter 4).

Isotopic analysis provided important insights into the autecology of willows and sedges, without requiring the destructive sampling of entire plants or root systems. The isotope research suggested willows received about 80% of their water from stream-related underground flows, while sedges received 50% of their water from rainfall (Chapter 7). Several lines of evidence suggested willow plant-root balances were being modified by herbivory. The improved physiological performance of browsed willows suggested improved root:shoot ratios (i.e., the aboveground area of willows were decreased faster than the belowground due to browsing, Chapter 7). But browsed willows growing away from streamside sites may have given up rooting depth and root biomass, based on their changes in isotopic signatures, thus reducing their access to groundwater compared to either protected willows or to willows growing on streamside sites (Chapters 7 and 8). Repeatedly browsed willows located away from streamsides thus likely became more vulnerable to intense herbivory through time.

Secondary metabolites of plants, including phenolics and tannins in willows, may function as a defense to plants against herbivores by binding with metabolites such as nitrogen-containing proteins, amino acids, DNA and RNAs, making them difficult to digest. Phenolics may be toxic and/or act as feeding deterrents (Robbins 1993). The research team, especially Brigham Young University scientists, studied the responses of tannins and phenolics to water amendment, clipping treatments, and ambient levels of browsing. The responses of secondary metabolites in willows to a variety of stratifications (tall, short; deeper vs. shallow water tables) and treatments (clipping, water amendments) are presented in Chapter 9. In general, willows clipped at intermediate (for clipping treatments) levels of 50% inside of one long-term exclosure in RMNP were able to respond in a predicted fashion by increasing production of tannins and phenolics over unclipped controls, but willows clipped at 100% removal of current annual shoot growth could not increase production of the secondary metabolites (Singer et al. 1998b). Less vigorous willows in Yellowstone National Park, growing on drier and less favorable sites, were not able to increase production of metabolites at either clipping treatment (Singer et al. 1998b).

The Role of Water Availability and Precipitation

There was compelling evidence for the large importance of water availability to the status of riparian plants on the RMNP winter range. The best evidence for this is descriptive and correlational, and the statistical model evidence, although present, is weak. Our check dams, although their effects were of shorter duration (only about six weeks) and of lesser magnitude than a beaver dam, resulted in a near doubling of herbaceous biomass and verified the importance of water (Chapter 4). Since 1946, total stream length declined 44–56% and surface area of water declined 47–69% on the elk winter range (Chapter 2); changes that were likely of enormous biological importance to the dewatering of large areas of willows and riparian vegetation. Rocky Mountain willows often regenerate in abandoned beaver ponds (Cottrell 1995) and the water and ice of the pond may have thwarted elk access to some willows and reduced herbivory. Shrub and herbaceous annual productions were correlated to March-September precipitation in a quadratic relationship, implying production increased with increasing precipitation to a threshold point, but above that point production did not further increase (Chapter 4). Stream flows and water tables were also higher following high winter snowpacks and high spring runoff and, therefore, streamside water tables were higher in those years. Shallower depths to the water table positively influenced herbaceous production. Depth to water was included in two best biological models that explained willow growth, but not in two other models (Chapters 4 and 12), although depth to the water table in June was correlated to willow growth (Chapter 12). These analyses present evidence for influence of depth to the water table to willow growth, even over the relatively narrow range of water tables that were investigated. The multivariate models suggested elk had a much larger influence on willow growth parameters than did depth to the water table for the range in water tables studied (based on better Akaike's Information Criteria values; Chapter 12).

Climate change might also have contributed to declines in willow growth and, ultimately, to declines in willow abundance. The winter range and the town of Estes Park have apparently experienced a minor, several-decade, warmer (0.89°C warmer) and drier (1 cm less precipitation) climate trend that was punctuated since 1995 with a wetter trend (Singer et al. 1998b). During our study, elk herbivory had the greatest negative effect on willows during a year with normal snowpack and runoff, but less effects during wetter years.

Ecosystem Sustainability and Fertility

The central question in the sustainability view of evaluating the abundance of ungulates is whether total plant production, both above and below ground, and soil fertility are maintained under the grazing level in question. The research indicated that elk were apparently depositing roughly equivalent amounts of N to what was being lost in the upland grass/shrub type. Additionally there was also slightly more root production and root N yield on grazed sites in this type, suggesting aboveground biomass was not being supported at the expense of the belowground biomass on grazed sites (Chapter 11). Soil bulk densities were higher on grazed sites (Chapter 10). The steeper slopes in the upland type might be vulnerable to accelerated soil loss due to ungulates since grazed sites exceeded the suggested thresholds (38% bare ground, 1.10 g/cm^2 bulk densities) of Packer (1963) for accelerated erosion. But this cannot be assessed, since we did not study sediment yields.

Elk activity apparently resulted in a loss of N from both the willow and aspen types. Nitrogen concentrations were higher in willow litter falling on grazed sites, but this did not compensate for other losses in the willow type (Chapter 11). Total biomass of leaf litter was less on grazed willow sites, willow sizes and production were reduced, herbaceous production was 22% less, and elk consumed 33% of the annual shrub biomass and 55% of the annual herbaceous biomass (Chapters 4 and 12). We calculated that total N inputs to the ground surface were only 5.79 g N/m^2/year on the grazed sites and 9.66 g N/m^2/year on ungrazed sites in the willow type. Apparently, because of the elk herbivory, N mineralization rates were substantially (79%) less and N pools (NO_3) were 78% less on grazed vs. ungrazed sites in the short willow type. Our analysis indicated elk activity also resulted in a net loss of N from the aspen type of 0.60 g N/m^2/year (1.13 g N/m^2/year was removed by elk grazing plus 0.53 g N/m^2/year was added in the form of elk urine and feces; Chapter 11). The evidence for declining fertility in grazed willow and aspen communities included: (1) the lower observed N mineralization and N pools; (2) the lower estimated N inputs to grazed sites; (3) the feeding behavior of elk; (4) CENTURY soil modeling of the observed parameters; and (5) the predictions of Biondini et al. (1998). Lowered N availability may reduce productivity and alter plant community composition.

Plants may compensate for tissue losses due to herbivory in a variety of ways. For example in grasslands grazed by native ungulates, increased rates of uptake of N by roots is often observed, as are increased N concentrations in shoots, increased N mineralization rates in the soil, and at times, increased N yield per unit of plant (Ruess 1984; Jaramillo and Detling 1988; Coughenour et al. 1990). These responses may be due to: (a) the conversion by ungulate grazing of less mobile N locked up in litter and standing dead vegetation, into more useable N in ungulate feces and urine; and/or (b) the reduction of soil microbial biomass due to reduced underground reserves. Grazed shrubs may possess an increased number of branched shoots, larger shoots that regrow following browsing, longer shoots, and more buds (Bergström and Danell 1987). These compensatory responses may be sufficient in some instances to result in higher net primary production (i.e., grazing optimization in moderately grazed vs. ungrazed controls (McNaughton 1979, 1983, 1993; Dyer et al. 1993; Frank and McNaughton 1993; Turner et al. 1993; Green and Detling 2000), but not in heavily grazed shrubs.

Compensatory processes were observed in browsed willows in the study. More willow shoots and more leaves were produced per unit of total biomass on browsed willows, more current year's biomass was produced per unit of the previous year's biomass, previously browsed shoots were longer and heavier, and a higher proportion of the total willow plant N was allocated to new leaves and new shoots in browsed plants (Chapter 5). Thus, RMNP supports a gradient of willow patches that vary in herbivory effects from some patches that are essentially unbrowsed, to some patches that are moderately browsed with high vigor, to other willow patches that are intensely browsed and negatively influenced by the browsing. Overall, 71% of all the willow patches on the park's winter range are now in the short willow type, an apparent browse-induced type, suggesting large areas of willows are browsed too much. The ecosystem functional, structural, and community alterations by ungulates of this shrub community are substantial.

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PART I

EMPIRICAL FINDINGS